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Four scenarios in which shadow competition should be prominent and factors affecting its strength

Inon Scharf[1] and Graeme D. Ruxton[2]

[1]School of Zoology, The George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel
[2]School of Biology, University of St. Andrews, St. Andrews, Scotland, UK

Correspondence: Inon Scharf (scharfi@tauex.tau.ac.il)

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Shadow competition is the interception of moving prey by a predator closer to its arrival source, preventing its availability to predators downstream. Shadow competition is likely common in nature, and unlike some other competition types, has a strong spatial component (with the exception of competition for space, which clearly also has a spatial component). We used an individual-based spatially-explicit simulation model to examine whether shadow competition takes place and which factors affect it in four scenarios considering ambush predators and active prey. First, when prey capture is uncertain ('the ricochet effect'). Here, the strength of shadow competition increases when it is harder to capture prey after the first unsuccessful capture attempt, whereas shadow competition is moderated if capture success is higher in successive attempts. Second, shadow competition becomes stronger when predators can capture prey arriving only from certain directions. Third, when prey tend to move along a barrier after encountering it. Here, predators located along this barrier may be more successful than those at random positions, but shadow competition in this scenario drastically decreases the capture success of predators in central positions along a barrier (i.e. having more than a single neighbor). Finally, in three-level systems of plants in clusters, herbivores searching for plants, and predators ambushing herbivores inside plant patches, predators with ambush locations in the periphery of plant patches are more successful than those at the patch center, especially at high predator densities. Our simulation indicates that shadow competition is plausibly relevant in various scenarios of ambush predators and prey, and that it varies based on the habitat structure and capture probability of prey by predators as well as the change in capture probability with successive encounters.

Keywords: foraging, movement ecology, ricochet effect, shadow effect, sit-and-wait predators, thigmotaxis

Introduction

The majority of research on competition focuses on either exploitation or interference competition (Anholt 1990, Mitchell et al. 1990, Cerdá et al. 2013). Shadow

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competition, occurring when 'an individual experiences reduced resource capture because resource relative-movement trajectories lead to prior interception by competitors', is probably much more common in nature than its rare consideration in the scientific literature implies (Scharf and Ruxton 2023a). In past literature, it has been considered as a special type of both exploitation and interference competition (Linton et al. 1991, Lubin et al. 2001, Elliott 2002, Louhi et al. 2014). Shadow competition should be a typical cost of living in groups (reviewed by Krause and Ruxton 2002). In the few cases where shadow competition has been investigated, the study system comprised sit-and-wait predators and mobile prey (Rayor and Uetz 1990, Linton et al. 1991, Lubin et al. 2001). Shadow competition leads to predators in the cluster's center receiving fewer prey than those in the cluster's periphery (Rayor and Uetz 1990, Gotelli 1997, Elliott 2002). Consequently, predators in central positions should relocate to reach more profitable ambush positions (Linton et al. 1991, Elliott 2002, Scharf 2020). In some cases, affected interior individuals show aggression toward those in peripheral positions (Hart 1986). Interference and exploitation also strengthen with the increase in spatial proximity among competitors (M'Gonigle et al. 2012, Fibich et al. 2014). Shadow competition is, however, fundamentally different from interference and exploitation because it is asymmetrically based on positions: predators closer to the arrival source of prey receive more prey flux and affect those located downstream much more strongly than vice versa (Scharf and Ruxton 2023a). This effect is probably the greatest when predators are adjacent and attenuates quickly.

Perhaps because shadow competition is a spatial phenomenon, it has been often examined using spatially-explicit individual-based models (Linton et al. 1991, Lubin et al. 2001, Morrell and Romey 2008, Scharf 2020). These models, together with a few experiments, led to several findings regarding the factors potentially strengthening or moderating shadow competition. For example, simulation models suggest that shadow competition should be stronger when prey move non-directionally (turn more frequently) than directionally. This occurs because such a movement pattern keeps the prey longer in the cluster's periphery, enabling predators there to capture them (Hein et al. 2004, Scharf 2020). Second, an experiment suggests that non-certain capture of prey (i.e. when an encounter between prey and predator does not lead to certain prey capture) should moderate shadow competition because it allows the prey to move into the cluster's center (Rao 2009). The latter phenomenon of uncertain capture is often termed 'the ricochet effect' (Rypstra 1989, Uetz 1989).

In a recent paper, Scharf and Ruxton (2023a) suggested several directions for further examination of shadow competition. The first is related to the ricochet effect. One could think of three ricochet effects: 1) an equal probability to be captured with successive encounters, or the prey has the same probability to be captured in each encounter, regardless of its history of previous encounters; 2) an increasing probability to be captured with successive encounters owing to, for instance, fatigue, injury, or prey becoming more apparent to other predators (Baker and Zemel 2000, Pruitt et al. 2009, Rao 2009); and 3) a decreasing probability to be captured owing to elevated prey vigilance or other behavioral changes driven by surviving an initial encounter (Lima et al. 2003, Beauchamp 2007, 2020). The consequences of these three ricochet effects for shadow competition may differ: the second type should moderate shadow competition the most, followed by the first type, and the third type should have an opposite effect.

The second suggested possible research direction concerns a scenario in which prey capture is influenced by the orientation of the predator relative to the trajectory of the prey. In such a situation the predators should face a specific direction from which prey most commonly arrive in order to capture them (e.g. marine sessile animals; Patterson 1984). Scharf and Ruxton (2023a) suggest that in peripheral positions the prey more frequently arrive from the same direction compared to central positions. Assuming that predators can change the direction that they face with experience, such a scenario can intensify shadow competition.

The third and fourth suggested research directions add complexity by allowing the prey to change its movement pattern in response to changing conditions. Many animals tend to move along encountered barriers, such as walls, rocks or fallen wood (Creed and Miller 1990, Besson and Martin 2005, Dussutour et al. 2005). This wall-following behavior (also known as thigmotaxis or centrophobism) is interpreted in different ways, from anxiety in vertebrates to exploration and desire to find an exit from an enclosure in insects (Santucci et al. 2008, Soibam et al. 2012, Johnson and Hamilton 2017). In any case, predators ambushing along such barriers may have higher capture success (Reinert et al. 1984, Scharf et al. 2021). However, the barrier can be perceived as shrinking the habitat to a single dimension, and predators downstream along the barrier should encounter fewer prey than those upstream, with the effect being even stronger than shadow competition in two or three dimensions.

Another reason for the prey to change its movement pattern is to efficiently gather its own resources. A general example is three-level systems of ambush predators, mobile herbivores and plants (or top predators, mesopredators and prey). Two good examples of such systems are those of crab spiders, bees and flowers, web-building spiders, grasshoppers and herbs/grass (Morse 1984, Schmitz et al. 1997). When plants are clustered in patches and if herbivores can move between patches and feed from more than a single plant, the best search pattern of herbivores is to use directional movement among patches and more tortuous movement within them, upon encounter of a plant ('area-restricted search'; Benhamou 1992, Dorfman et al. 2022). Then, the best ambush locations of predators should be in plant patches, because herbivores spend longer time inside patches than outside patches (Scharf 2021). However, here too, shadow competition may come into play, as peripheral positions of ambush predators in plant patches should be superior to central ones.

Material and methods

We use the ODD protocol to describe our individual-based model (Grimm et al. 2006, 2010).

Purpose

Our goal was to examine whether all the above-mentioned four scenarios indeed result in shadow competition and more importantly whether shadow competition is increased or moderated as predicted. Specifically, we examined how 1) different ricochet effects, 2) limiting the direction from which predators can attack prey, 3) prey movement along barriers and 4) the usage of area-restricted search, should either increase or moderate the strength of shadow competition.

Entities, state variables and scales

Entities

Scenarios 1–3 of the simulation comprise two entities: ambush predators and mobile prey. Scenario 4 refers to the prey as herbivores, and includes another entity consumed by herbivores: plants (three trophic levels in total). The level of interest is the ambush predators.

State variables

The state variables are positions within the grid, the prey movement directions, the movement directionality levels of prey (the probability to keep moving in the current direction), whether prey are alive or dead (i.e. have been already captured by predators), how many prey items each predator caught, and in scenario 4 also plant positions and whether they are alive or dead (i.e. have been consumed by herbivores). Dead prey/herbivores/plants remain dead until the simulation ends.

Scales

The grid/arena is 100 × 100 space units. The grid is homogenous except for the distance of each cell to the nearest edge. The simulation runs until all prey (or herbivores in scenario 4) are captured by predators. The grid should be equivalent to a cluster of ambush predators located in a microhabitat. The number of time steps required to cross the arena from one side to another is equivalent to the time required to cross the microhabitat.

Process overview and scheduling

Uncaptured prey moved one cell each time step to one of the four adjacent cells (left, right, up or down). Using four instead of eight movement directions in grid-based models is probably better because the distance moved each step is identical (1 space unit in contrast to $\sqrt{2}$ when moving along a diagonal) and because it avoids the complexity of dealing with two types of adjacent cells (orthogonal and diagonal; Birch 2017). Furthermore, a turn of 45° is different from 90° influencing not only the distance but also the movement directionality level. The prey had a constant probability (0.8) to keep moving in the same direction as previously, and the rest of the probability was evenly split between turning to their left or right (relative to their previous direction). A move was then implemented. If it meant that the prey left the arena, another prey appeared in a random place at one of the arena's edges with its movement direction allocated stochastically as at the beginning of the simulation ('absorbing boundaries'). This is because we wished prey to disappear only owing to predation events. This way of dealing with the arena boundaries is more realistic than using a 'torus model' (the prey reappears from the other side creating a 'doughnut-shaped arena'), which creates a three-dimensional landscape, although 'absorbing boundaries' interferes to some extent with the prey movement directionality. Predators never moved in the simulation. A predator potentially catches a prey when their positions overlap (i.e. when they both coincide in the same grid location due to the prey individual moving into the cell where the sit-and-wait predator is located). See the Supporting information for flowcharts describing each of the four scenarios.

Design concepts

Basic principles

The designed model is spatially explicit, individual-based and grid-based. The simulation and all analyses were done in MATLAB (R2022b).

Fitness of ambush predators

Fitness was calculated differently in scenarios 1–2 and 3–4. In the first two scenarios, we ran the simulation with the same predators (or predator positions) five times. We calculated the distance of each predator to the nearest edge position. We evaluated the level of shadow competition by regressing the number of prey individuals captured by each predator during a single run of the simulation (five replications per predator, as the simulation was run five times) against its distance to the nearest arena edge. This procedure resulted in 150 data points (30 predators × 5 runs) and a regression slope. The steeper the obtained negative regression slope, the stronger the shadow competition. This is because a negative slope indicated that predators in the arena's periphery captured more prey than those in the arena's center, and this spatially-dependent variance increased as the slope became steeper. This procedure was repeated 100 times to acquire a sample size for among-treatment comparisons. In scenario 3 and 4 below, we treated predator positions as categorical (e.g. along a barrier or in a random location) and referred to the number of prey individuals captured as the response variable. Here, each predator location configuration was repeated only once, and each treatment was run 100 times.

Comparison among treatments

To compare among treatments, we calculated the 95% confidence intervals (CI) using bootstrapping for each 100 replications. We considered scenarios to produce different outcomes when their CIs did not overlap (similar to Scharf 2020, 2021). Using conventional inferential statistics to analyze the output of simulation models is not recommended due to the possibility of greatly enlarging the sample size making even negligible differences significant (Grimm and Railsback 2005, White et al. 2014).

Initialization

In scenario 1 and 2, predators (30) were initially located in random positions in the arena, subject to the restriction that each occupied a different position (Fig. 1a). Prey (300) were evenly allocated to each of the arena's four edges and placed there in random positions (one of 396 edge locations). Prey were independently stochastically assigned an initial movement direction (left, right, up or down), each with equal probability, but were not assigned the direction that would bring them on the next step out of the arena. In scenario 3, either 3, 5 or 7 predators, were located along one edge, defined as a 'barrier', and the rest (completing to 30 predators) were initially located in random positions (Fig. 1b). Prey (300) were allocated in this case to three of the four edges (no prey along the barrier). In scenario 4, plants (180) were located in three patches, each of 60 individuals (Fig. 1c). We chose random points as patch centers and then allocated an equal number of plants to each patch (at a random direction and a random distance of 0–10 units from the patch center). Herbivores (60) were placed on the arena's four edges in equal numbers. Half of the predators were placed in a random direction close to the first, second, or third patch centers (up to two units from the patch center) and the rest were placed in random directions farther away from the center of the three patches, but still within the patch boundaries (up to eight units from the patch center). The number of predators in scenario 4 was either 6, 12, 18 or 24.

Input

The model does not use input data to represent time-varying processes.

Scenario 1. The link between the ricochet effect and shadow competition

We first re-examined previous models demonstrating a decrease in shadow competition with increasing ricochet effect or when prey capture probability drops (Lubin et al. 2001, Scharf 2020). We compared certain capture (100%) to lower but constant capture probabilities (75, 50 and 25%). Next, we applied four treatments, all of which are varieties of the ricochet effect: 1) moderately increasing capture probability with successive encounters (50, 75 and 100% capture probability in the first, second and further encounters). 2) Strongly increasing capture probability with successive encounters (50 and 100% capture probability in the first and further encounters). 3) Moderately decreasing capture probability with successive encounters (75, 50 and 25% capture probability in the first, second and further encounters). 4) Strongly decreasing capture probability with successive encounters (75 and 25% capture probability in the first and

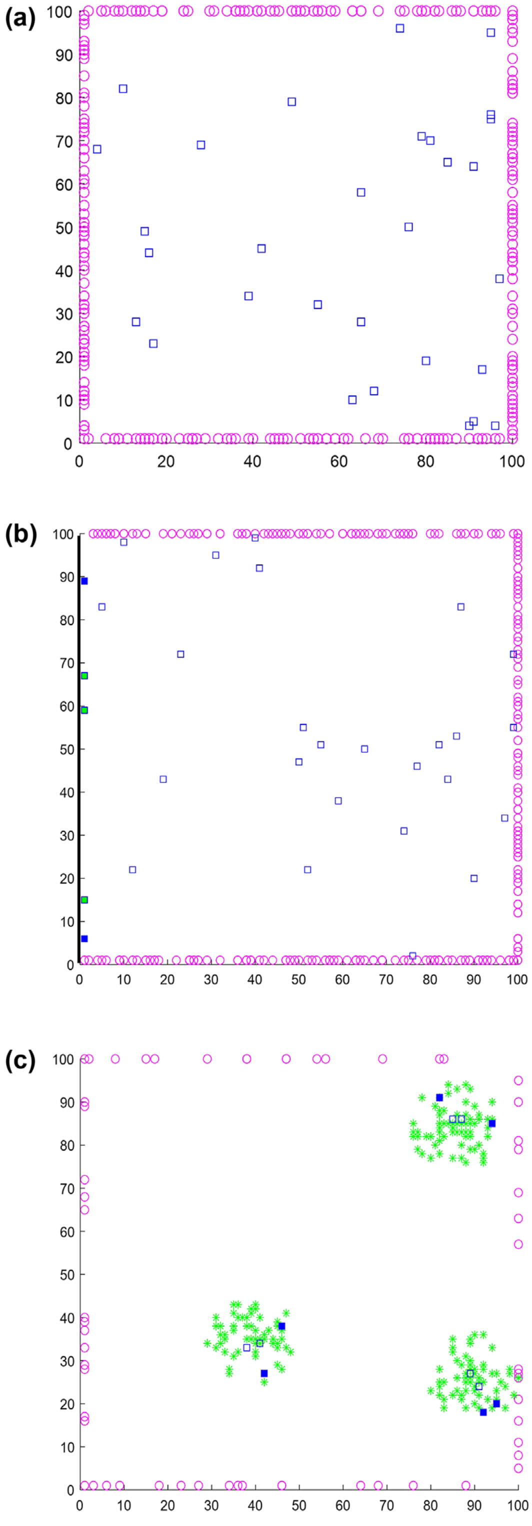

Figure 1. The opening situation of the simulation in (a) scenario 1 and 2, (b) scenario 3, and (c) scenario 4. Blue squares, pink circles, and green asterisks stand for the ambush predators, moving prey, and plants. In (b), the thick vertical line is the barrier, squares filled with blue are predators at barrier peripheral positions and squares filled with green are predators at barrier central positions. In (c), blue-filled squares and empty blue squares stand for predators in the plant patch periphery and center, respectively.

further encounters). Each time a prey item left the arena, the capture probability of its replacement assumed the replacement had never previously encountered a predator. Figure 2a presents a scheme for this scenario.

It is important to consider which null prediction to compare each scenario. The higher the frequency of missed captures, the weaker the shadow competition is. Thus, we had to evaluate the number of missed captures for each scenario for all runs and find the constant capture success that gave an equivalent number. The former was calculated based on the simulation itself. The latter was calculated based on a geometric series, giving a sum that is as similar as possible to the value obtained based on the simulation. The sum is $S=a_1/(1-q)$, where a_1 is the expected number of missed captures upon the first encounter and q is the probability of missed captures. Specifically, treatment 1 above resulted in an average number of 86.36 missed captures per simulation run. According to the above-mentioned formula, a fixed capture probability of 54.08% resulted in a similar number (254.7 missed captures). Thus, we compared treatment 1 to such a fixed capture probability. Similarly, treatment 2 was compared to a fixed capture probability of 57.2% (224.8 missed captures), treatment 3 to 71.31% (120.7 missed captures), and treatment 4 to 68.1% (140.4 missed captures).

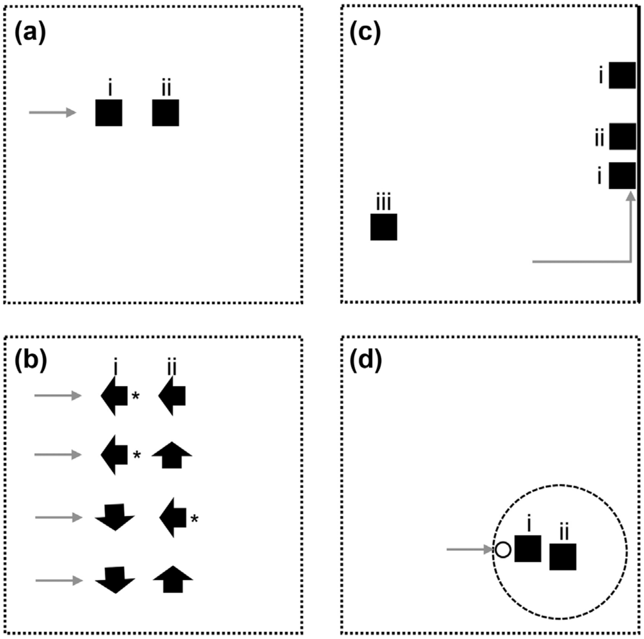

Figure 2. Schemes of all scenarios. (a) Scenario 1. The dotted squares represent the arena (100 × 100 cells), and the grey arrow stands for the prey and its movement direction. The two black squares stand for predators (i = upstream, ii = downstream). We applied four scenarios with either fixed probabilities of prey capture by predators, increasing probabilities with successive encounters, or decreasing ones. (b) Scenario 2. The thick arrows stand for predators and the direction they face (they can capture prey arriving only from this direction). The predator capturing the prey is marked with an asterisk. (c) Scenario 3. The prey (grey) starts moving along a barrier (thick black vertical line) after reaching it. We differentiate between predators on the barrier (i = barrier-peripheral positions, ii = barrier-central positions) and predators at random positions (iii). (d) In a three-level system, plants are aggregated in patches (dotted circle), where predators (black squares) should ambush herbivore prey (grey arrow). When herbivores encounter a plant (small circle), they switch to more tortuous movement, which makes positions in the patch periphery (i) more profitable for predators than those in its center (ii).

Scenario 2. The predator and prey face one another

Each predator was independently and stochastically allocated a direction of orientation, from four possible options, each with equal probability. If a predator is allocated the upward direction, then it is considered to face prey that enters its grid position downward (i.e. the prey is captured if its movement direction is opposite to the predator's facing direction). We applied two treatments (Fig. 2b): 1) the predator captures prey only if the predator and prey face one another; and 2) the predator captures prey if they face one another or if the predator faces the two adjacent directions (i.e. there is no capture only if the predator facing direction and the prey movement direction are identical). Based on previous results, decreasing capture probability moderates shadow competition. To account for that, treatment 1 was compared to an 'all directions' capture probability of 25% and treatment 2 to an 'all directions' capture probability of 75%, which are similar to the capture probability in treatments one and two, respectively.

Scenario 3. Prey moving along a barrier

Here, one of the four peripheral edges of the grid was designated as a barrier. Predators were either located immediately beside the barrier or at random positions in the arena. When more than two predators were located alongside the barrier, two predators were identified as barrier-peripheral while the rest were barrier-central (Fig. 2c). The prey began the simulation in one of the remaining three possible arena edges (initial location of prey along the barrier was not allowed). When the prey reached the barrier, it turned either right or left and moved along the barrier until it was either captured by a predator or left the arena. All other simulation characteristics were as in the 'basic simulation design'. The treatments were either 3, 5 or 7 predators along the wall and the rest (27, 25 or 23, respectively) in random locations.

Scenario 4. A three-level system of predators, herbivores and plants

We simulated a three-level system of predators, herbivores and plants (or top predators, mesopredators and prey; Fig. 2d). The plants were located in three patches, each of 60 individuals. We chose random points as patch centers and then allocated an equal number of plants to each patch (at a random direction and a random distance of 0–10 units from the patch center). Sixty herbivores were placed on the arena's four edges in equal numbers. Half of the predators were placed in a random direction close to the first, second, or third patch centers (up to two units from the patch center) and the rest were placed in random directions farther away from the center of the three patches, but still within the patch boundaries (up to eight units from the patch center). Only the herbivores moved whereas both plants and predators were sedentary. Prey had a constant 0.9 probability to keep moving in the same direction, until encountering a plant. Then, on encountering a plant this probability dropped to 0.5 for the next ten times steps (and the remaining probability evenly split between right and left turns) to induce more tortuous movement, before resuming more directional movement. This 'ten-steps' counter was reset every time a plant was encountered. The treatments comprised an increasing number of predators: 6, 12, 18 and 24. Note that in the first two scenarios encountering a predator does not necessarily mean capture, in contrast to the two last scenarios. All scenarios are summarized in Table 1.

Sensitivity analysis

The Supporting information comprises a comprehensive sensitivity analysis of all four scenarios. The goal of the sensitivity analysis is to moderately change parameters that are not thoroughly studied in the main model analysis and examine how they affect the model outcome (Grimm and Railsback 2005). To this end, we varied the number of prey and predators, the movement directionality level, and the number of plants (only in scenario 4). Most changes led only to quantitative changes but not qualitative ones, with a few exceptions. For example, the conclusions of scenario 1 did not hold if the prey movement was too directional. The conclusions of scenario 2 held partially when changing the number of prey or predators. See the Supporting information for a full sensitivity analysis.

Results

The link between the ricochet effect and shadow competition

First, lower capture probability when predators encounter prey moderated the regression slope of the number of prey individuals captured per predator regressed over the predator distance to the nearest arena edge, which is a proxy of shadow competition (Fig. 3a). When the capture probability of prey increases from the first predation attempt to later ones, shadow competition is lower than a comparable constant-capture probability (Fig. 3b; a difference of more than 20%). In contrast, when the capture probability of prey decreases from the first predation attempt to later ones, shadow competition is stronger than a comparable constant level of capture probability (Fig. 3c; a difference of around 14%). Thus, the ricochet effect is not a single phenomenon, and the way previous encounters change prey vulnerability has a strong influence on the strength of shadow competition.

The predator and prey face one another

When predators captured only prey arriving from a single direction, shadow competition was stronger than a comparable scenario of omnidirectional 25% capture probability (Fig. 4; a difference of over 20%). A scenario of capturing prey only from three directions did not differ from a comparable scenario of 75% capture probability (Fig. 4).

Prey moving along a barrier

Predators on the barrier periphery always captured the highest number of prey (Fig. 5; around double of other predators summed). That said, the success of the barrier-central predators differed depending on the total number of predators on the barrier: when only three predators are located along the barrier, the barrier-central predator captures more prey than predators in random positions within the arena (around 32% difference). When more predators are located along the barrier, barrier-central predators capture fewer prey than predators in random positions (around 16 or 28% difference in the other direction when five or seven predators are along the barrier).

A three-level system of predators, herbivores and plants

The predicted strength of shadow competition differed based on the number of predators simulated. With an increasing

Table 1. A brief summary of the simulation design according to scenarios

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Predators	30	30	30 (3, 5, 7[a])	6, 12, 18, 24[b]
Prey/herbivores	300	300	300	60
Plants	–	–	–	180
Directionality[c]	0.8	0.8	0.8[d]	0.9, 0.5[e]
Predator start positions	random	random	random or barrier	plant patch center/periphery
Prey start positions	four edges	four edges	three edges (but not the barrier)	four edges
Capture prob.	varying (0.25-1)	varying[f]	1	1
Resp. variable	slope [g]	slope	prey captured	prey captured

[a] 3, 5 or 7 predators were located along a barrier. [b] Half of the predators were located in the center of plant patches while the rest were at their periphery. [c] Directionality refers to the probability of keeping the current movement direction. [d] After reaching the barrier, the prey keeps moving along it. [e] The two numbers refer to movement before and after an encounter with a plant. [f] Capture is certain but only if the predator faces the prey's direction of arrival. [g] The slope, which represents the strength of shadow competition, is the number of prey captured regressed over the predator distance from the nearest arena's edge. Other factors, such as the arena size (100 × 100 cells) and simulation duration (until all prey is captured), are identical across scenarios.

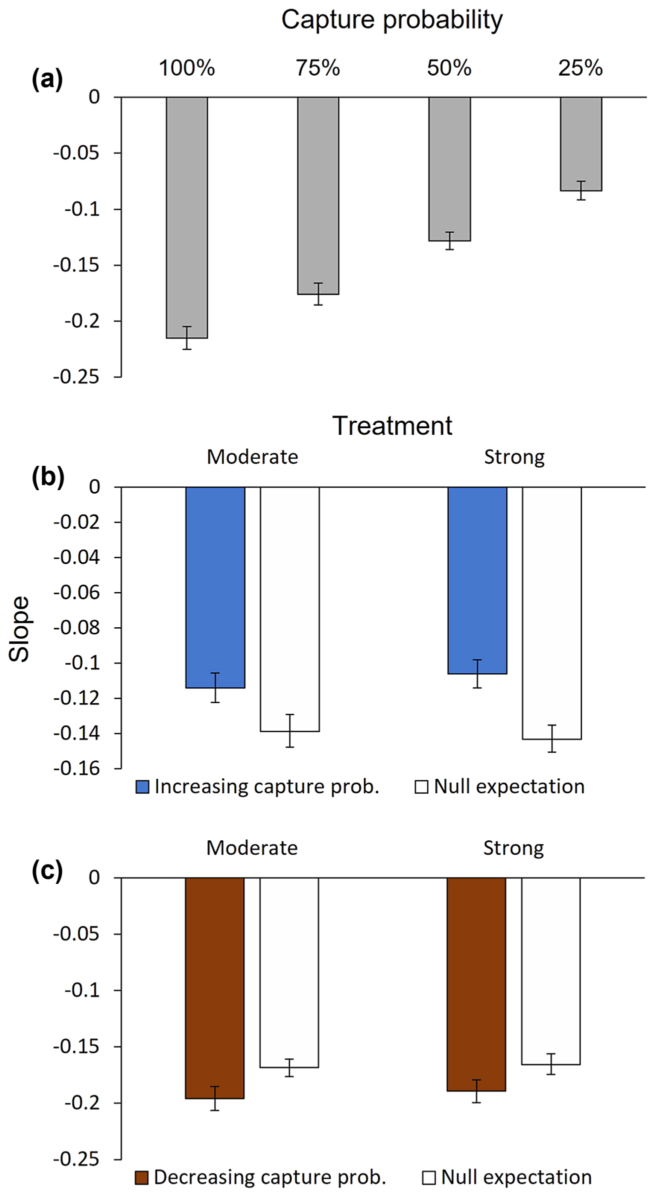

Figure 3. The strength of shadow competition (= slope) as a function of the ricochet effect and uncertain capture of prey. (a) The intensity of shadow competition decreases with the intensity of the ricochet effect or when the probability of prey capture declines. (b) Increasing capture probability with successive encounters (left, blue) either moderately (50, 75 and 100% capture probability on the first, second, and later capture attempts) or strongly (50 and 100% capture probability on the first and later capture attempts), compared to a null model of fixed capture probability (right, grey). Means ± 95% CI are presented. (c) Decreasing capture probability with successive encounters (left, brown) either moderately (75, 50 and 25% capture probability on the first, second, and later capture attempts) or strongly (75 and 25% capture probability on the first and later capture attempts), compared to a null model (right, grey).

predator number, the difference between predators in the plant patch periphery and those in the patch center increased: predators on the periphery captured more prey when the number of predators was sufficiently high (a difference of around 9 or 17% when the total number of predators was 18 or 24, respectively; Fig. 6).

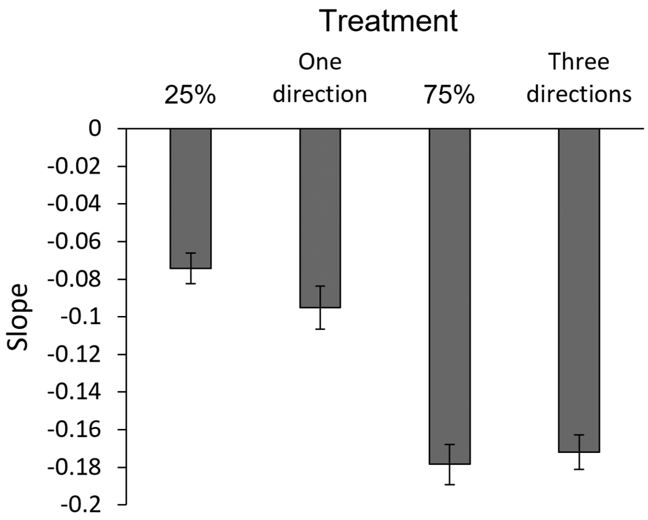

Figure 4. Shadow competition (= slope) gets stronger when predators can capture prey only if they face the prey movement direction, compared to a null model of a fixed 25% probability to capture prey. In contrast, enabling the predators to capture prey from all directions but the posterior one (three directions) does not differ from the null model of a fixed 75% capture probability. Means ± 95% CI are presented.

Discussion

We explore here four scenarios that affect the importance of shadow competition for the capture success of ambush predators hunting mobile prey. First, we demonstrate that the 'ricochet effect' (prey bouncing from the first ambush predator to the next) is not a single phenomenon and its

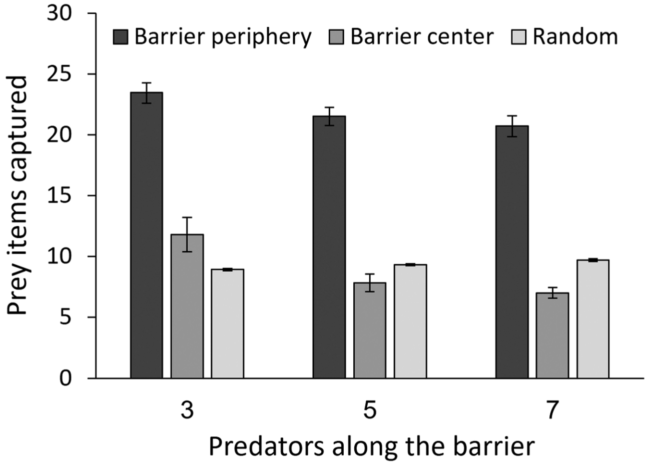

Figure 5. The relative success of predators along the barrier, when they have a single neighbor predator (barrier periphery; dark grey) or two (barrier center; medium grey) and at random locations in the arena (light grey) with increasing numbers of predators along the barrier (3, 5, or 7 of 30 in total). Means ± 95% CI are presented.

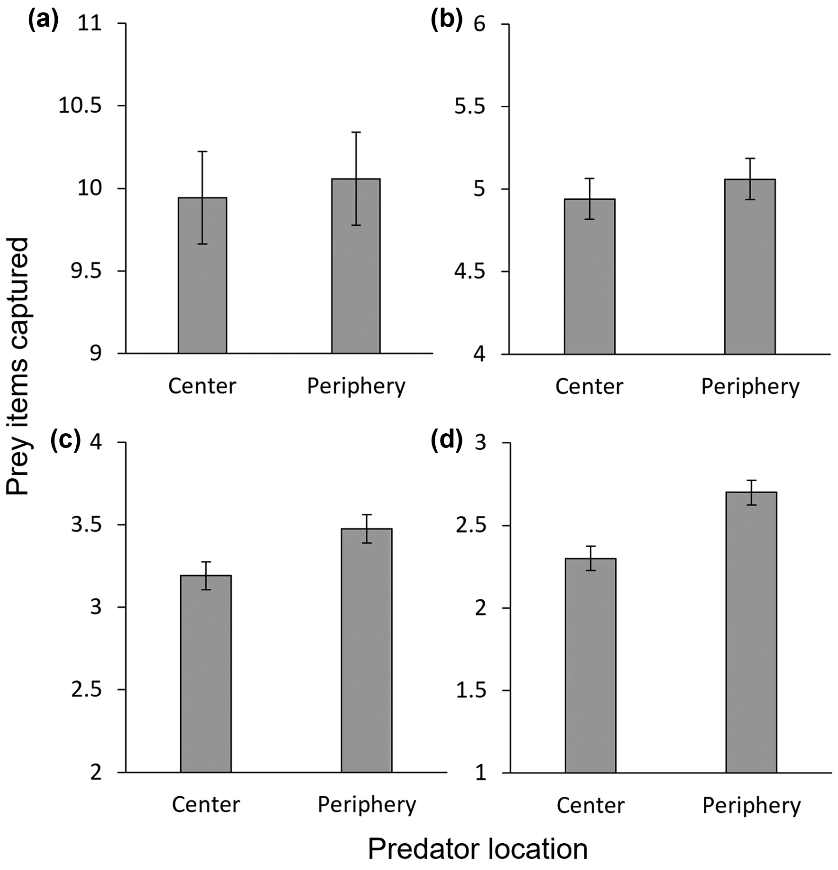

Figure 6. The success of predators ambushing herbivore prey in the center versus periphery of plant patches. (a) Six, (b) twelve, (c) eighteen or (d) twenty-four predators in total, evenly allocated to positions in the plant patch center or periphery. Means ± 95% CI are presented.

interaction with shadow competition depends on the detail of whether capture probabilities increase or decrease with successive capture attempts, both of which are likely system-specific. Second, when predators can hunt only when they face the prey's arrival direction (or more generally if predators can only capture prey approaching from a narrow range of directions), shadow competition intensifies and there is an advantage for predators located at the cluster periphery. Third, when predators are located along a barrier, and prey move along the barrier after encountering it, predators at the barrier periphery are much more successful than those located near its center. This effect is due to shadow competition. The central barrier individuals' success is even lower than predators located at random positions away from the barrier when the number of predators along the barrier is sufficiently high. Fourth, in a three-level system of predators, herbivores and plants, when plants are clustered and herbivores use area-restricted search to locate plants (a switch to more tortuous movement upon first encounter), predators should be located inside plant patches to maximize their capture rates. However, predators should not be located too deep inside the plant patch, as predators in the cluster periphery are more successful in hunting herbivores, owing to shadow competition, especially when the number of predators is sufficiently high.

The link between the ricochet effect and shadow competition

Our simulation results demonstrate that the 'ricochet effect' is an umbrella term for several processes, which may differentially affect shadow competition. First, uncertainty in the capture success of prey moderates shadow competition, as suggested in models and experimentally demonstrated (Rao 2009, Scharf 2020). The less certain the capture is, the lower the shadow competition is. However, the 'ricochet effect' sometimes does not mean an equally uncertain capture in all encounters, but either an increasing capture probability with repeated encounters, or a decreasing one. An increasing capture probability with successive encounters moderates shadow competition even further compared to a scenario of fixed capture probability. This process takes place as failed captures increase future capture probabilities by predators, which are farther away from the cluster periphery. Such an increase in capture probability is possible owing to fatigue of the prey, its injury, if it is slowed down, or if failed capture attempts attract the attention of other predators nearby or increase their vigilance. It is no surprise that fatigue or injury increases predation risk (Ota 2018, Diniz 2020), or that predation success of ambush predators decreases with increasing movement speed of the prey (Van Damme and Van Dooren

1999, Clemente and Wilson 2016). In addition, injury impairs the prey's movement or maneuverability, which leads to higher predation success (Downes and Shine 2001, Krause et al. 2017). A decreasing capture probability, which intensifies shadow competition, is possible due to elevated prey vigilance or simply seeking refuge after the first failed attempt. This process takes place as a failed capture decreases future capture probabilities by predators farther away from the cluster periphery. Thus, to correctly evaluate the strength of shadow competition, one should first identify the type of the 'ricochet effect' taking place in the studied system.

The predator and prey face one another

A scenario in which the predator captures the prey only when they face one another occurs in several contexts. Most animals have a limited area of binocular vision, which enables better distance estimation, and vision is rarely symmetrical in all directions (Jackson and Pollard 1996, Cronin 2005). Thus, visual predators are probably better able to capture prey arriving from certain directions better than others. The simulation results suggest that when the preferred attack direction (or field of vision) is narrow, predators at the cluster periphery should have a stronger advantage over those in the center, thus elevating shadow competition. Orientation-related capture probability could be driven by other mechanisms than binocular vision. It may relate to the non-isotropic ability of the predator to pounce on or restrain prey before the prey can deploy anti-predator defenses (Bhattacharyya et al. 2021). The model assumes that predators should change their orientation to the arrival direction of the last prey. Assuming a change of orientation following an unsuccessful encounter is reasonable too. Trap-building predators, for example, respond to unsuccessful encounters by increasing their trap dimensions (Lomáscolo and Farji-Brener 2001, Nakata 2007, Scharf et al. 2010). As prey arrive from more random directions in the cluster center than in its periphery, where prey arrive most frequently from the nearest edge, facing a single direction only is less determinantal for predators in the cluster periphery than in the center.

Prey moving along a barrier

Animal movements along a barrier, such as logs, rocks, or walls, are common in both vertebrates and invertebrates for diverse reasons (Introduction). However, only a few studies examined either empirically or theoretically how such a movement pattern should affect predation probabilities (Reinert et al. 1984, Scharf et al. 2021). Sit-and-wait predators benefit from ambushing prey along barriers, but only when the predators along the barriers are not too dense. The key prediction generated here is the strong difference between peripheral positions along barriers and more central ones. Central barrier positions, especially under high predator density, might be even inferior to positions away from the barrier. Thus, the quality of ambush positions along a barrier can deteriorate fast, from being an above-average position to a below-average position, due to increasing predator density on the barrier. This scenario suggests pressure for the ambush predators to monitor their gain and relocate if the gain falls below the average gain of their habitat (Olive 1982, Scharf and Ovadia 2006), which is similar to what is expected of widely foraging predators (Charnov 1976). It is unclear how well ambush predators can follow such changes and especially separate between a global decline in prey (e.g. season poor in prey) versus a local decline triggered by the positions of other predators (predators settling upstream, closer to the source of prey arrival; Scharf et al. 2009). The key might be a gradual versus abrupt decrease in prey arrival, which is perhaps interpreted as temporal versus spatial shortage, leading to relocation in the latter case and no response in the former, as demonstrated in spiders and antlions (Vollrath 1985, Jenkins 1994).

A three-level system of predators, herbivores and plants

Many herbivores use directional movement among plant patches and tortuous movement within them, termed area-restricted search (reviewed by Dorfman et al. 2022). In three-level systems, the predators' interest is to spatially follow their herbivore prey (Sih 2005), and they should therefore ambush prey within such patches. Here too, we demonstrated a potential for shadow competition, as herbivores are captured more by their predators ambushing them at the periphery of the plant patches rather than in the patch centers. This pattern intensifies with predator density and should eventually lead to predators either relocating to the patch periphery and then perhaps even out of patches. This may lead to changes in the herbivores' movement patterns or their tendency to use area-restricted search and have implications for the foraging success of the herbivores, as well as selection for or against aggregation of plants (Scharf 2021).

Summary of the model predictions

In order to facilitate putting the predictions of our model to a test empirically, we briefly summarize here the main predictions according to scenarios. Scenario 1 suggests that when prey capture by predators is not certain, the strength of shadow competition should depend on whether prey become more alert after the first encounter, and then harder to capture (strengthening shadow competition), or slower/fatigued after first capture, making it more easily captured next (weakening shadow competition). Scenario 2 suggests that shadow competition should intensify when predators must face the prey in order to capture it, and the more limited the field of view of predators, the stronger shadow competition is expected to become. Scenario 3 presents the superiority of predator positions along a barrier, if prey follow the barrier after reaching it, compared to predators not along a barrier. However, the superiority of barrier-adjacent locations diminishes if they are centrally located along the barrier and possess neighbors from both sides. At higher predator densities, predators away from barriers are expected to be more successful than those in the central barrier positions. Finally, the use of area-restricted search by prey should result in shadow competition, which intensifies with predator density.

Final words

Our goal was to highlight four general case studies, in which shadow competition may exist and depend on local conditions, and which are worthwhile for empirical research. Our intention was not to point to specific parameter ranges, but to qualitatively describe such scenarios. As with most models, our model has many simplifying assumptions. For example, the simulated habitat is homogenous except for the modeled parameters (e.g. a barrier), constant behavior (e.g. prey movement) during each simulation run, no satiation of predators, and no variation within the predator or prey population, except for their spatial positions. Some computation decisions may also be contested, such as our use of absorbing boundaries, basing predator success only on the prey number they catch, or using four instead of eight movement directions (discussed by Birch 2006, Birch et al. 2007). Adjusting the model to specific systems in nature requires examining whether the model's simplifying assumptions hold and adjusting the model otherwise. It is common to assume that ecological models trade off generality, precision and realism (Levins 1966), and our model sacrifices both precision and realism for generality. It is also important to note that individual-based simulation models, like the one presented here, are mere tools to raise more sophisticated predictions or provide mechanisms for already observed phenomena (Schmitz 2000, DeAngelis and Grimm 2014). Testing the model's main outcomes or predictions should be the next step to examine how useful it is in pointing to cases in which shadow competition takes place in nature. Another fruitful direction should be to allow both predators and prey to change their strategies in response to one another and make their decisions fitness based.

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Author contributions

Inon Scharf: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – original draft (equal). **Graeme D. Ruxton**: Formal analysis (equal); Investigation (equal); Writing – original draft (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0rxwdbs66 (Scharf and Ruxton 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Anholt, B. R. 1990. An experimental separation of interference and exploitative competition in larval damselfly. – Ecology 71: 1483–1493.

Baker, M. B. and Zemel, A. 2000. Josef Bertrand catches some ants: unbiased random trajectories for the simulation of position effects in groups. – J. Theor. Biol. 207: 299–303.

Beauchamp, G. 2007. Vigilance in a selfish herd. – Anim. Behav. 73: 445–451.

Beauchamp, G. 2020. Predator attack patterns influence vigilance in a virtual experiment. – Behav. Ecol. Sociobiol. 74: 49.

Benhamou, S. 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. – J. Theor. Biol. 159: 67–81.

Besson, M. and Martin, J. R. 2005. Centrophobism/thigmotaxis, a new role for the mushroom bodies in *Drosophila*. – J. Neurobiol. 62: 386–396.

Bhattacharyya, K., McLean, D. L. and MacIver, M. A. 2021. Intersection of motor volumes predicts the outcome of ambush predation of larval zebrafish. – J. Exp. Biol. 224: jeb235481.

Birch, C. P. D. 2006. Diagonal and orthogonal neighbours in grid-based simulations: Buffon's stick after 200 years. – Ecol. Modell. 192: 637–644.

Birch, C. P. D., Oom, S. P. and Beecham, J. A. 2007. Rectangular and hexagonal grids used for observation, experiment and simulation in ecology. – Ecol. Modell. 206: 347–359.

Cerdá, X., Arnan, X. and Retana, J. 2013. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. – Myrmecol. News 18: 131–147.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Clemente, C. J. and Wilson, R. S. 2016. Speed and manoeuvrability jointly determine escape success: exploring the functional bases of escape performance using simulated games. – Behav. Ecol. 27: 45–54.

Creed, R. P. and Miller, J. R. 1990. Interpreting animal wall-following behavior. – Experientia 46: 758–761.

Cronin, T. W. 2005. The visual ecology of predator-prey interactions. – In: Barbosa, P. and Castellanos, I. (eds), Ecology of predator–prey interactions. Oxford Univ. Press, pp. 105–138.

DeAngelis, D. L. and Grimm, V. 2014. Individual-based models in ecology after four decades. – F1000prime Rep. 6: 39.

Diniz, P. 2020. Opportunistic predation reveals a hidden cost of fighting in birds. – Ornithol. Res. 28: 178–180.

Dorfman, A., Hills, T. T. and Scharf, I. 2022. A guide to area-restricted search: a foundational foraging behaviour. – Biol. Rev. 97: 2076–2089.

Downes, S. and Shine, R. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? – Ecology 82: 1293–1303.

Dussutour, A., Deneubourg, J. L. and Fourcassié, V. 2005. Amplification of individual preferences in a social context: the case of wall-following in ants. – Proc. R. Soc. B 272: 705–714.

Elliott, J. M. 2002. Shadow competition in wild juvenile sea-trout. – J. Fish Biol. 61: 1268–1281.

Fibich, P., Lepš, J. and Weiner, J. 2014. Individual variability and mortality required for constant final yield in simulated plant populations. – Theor. Ecol. 7: 263–271.

Gotelli, N. J. 1997. Competition and coexistence of larval ant lions. – Ecology 78: 1761–1773.

Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.

Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based models. – Ecol. Modell. 198: 115–126.

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J. and Railsback, S. F. 2010. The ODD protocol: a review and first update. – Ecol. Modell. 221: 2760–2768.

Hart, D. D. 1986. The adaptive significance of territoriality in filter-feeding larval blackflies (Diptera: Simuliidae). – Oikos 46: 88–92.

Hein, S., Pfenning, B., Hovestadt, T. and Poethke, H.-J. 2004. Patch density, movement pattern, and realised dispersal distances in a patch-matrix landscape – a simulation study. – Ecol. Modell. 174: 411–420.

Jackson, R. R. and Pollard, S. D. 1996. Predatory behavior of jumping spiders. – Annu. Rev. Entomol. 41: 287–308.

Jenkins, B. A. 1994. The behavioural response of the antlion *Myrmeleon pictifrons* to a sudden change in prey capture rate. – Acta Oecolog. 15: 231–240.

Johnson, A. and Hamilton, T. J. 2017. Modafinil decreases anxiety-like behaviour in zebrafish. – PeerJ 5: e2994.

Krause, J. and Ruxton, G. D. 2002. Living in groups. – Oxford Univ. Press.

Krause, J., Herbert-Read, J. E., Seebacher, F., Domenici, P., Wilson, A. D. M., Marras, S., Svendsen, M. B. S., Strömbom, D., Steffensen, J. F., Krause, S., Viblanc, P. E., Couillaud, P., Bach, P., Sabarros, P. S., Zaslansky, P. and Kurvers, R. H. J. M. 2017. Injury-mediated decrease in locomotor performance increases predation risk in schooling fish. – Phil. Trans. R. Soc. B 372: 20160232.

Levins, R. 1966. The strategy of model building in population biology. – Am. Sci. 54: 421–431.

Lima, S. L., Mitchell, W. A. and Roth II, T. C. 2003. Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. – Evol. Ecol. Res. 5: 1083–1102.

Linton, M. C., Crowley, P. H., Williams, J. T., Dillon, P. M., Aral, H., Strohmeier, K. L. and Wood, C. 1991. Pit relocation by antlion larvae: a simple model and laboratory test. – Evol. Ecol. 5: 93–104.

Lomáscolo, S. and Farji-Brener, A. G. 2001. Adaptive short-term changes in pit design by antlion larvae (*Myrmeleon* sp.) in response to different prey conditions. – Ethol. Ecol. Evol. 13: 393–397.

Louhi, P., Mäki-Petäys, A., Huusko, A. and Muotka, T. 2014. Resource use by juvenile brown trout and Alpine bullhead: influence of interspecific versus intraspecific competition. – Ecol. Freshwater Fish 23: 234–243.

Lubin, Y., Henschel, J. R. and Baker, M. B. 2001. Costs of aggregation: shadow competition in a sit-and-wait predator. – Oikos 95: 59–68.

M'Gonigle, L. K., Mazzucco, R., Otto, S. P. and Dieckmann, U. 2012. Sexual selection enables long-term coexistence despite ecological equivalence. – Nature 484: 506–509.

Mitchell, W. A., Abramsky, Z., Kotler, B. P., Pinshow, B. and Brown, J. S. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. – Ecology 71: 844–854.

Morrell, L. J. and Romey, W. L. 2008. Optimal individual positions within animal groups. – Behav. Ecol. 19: 909–919.

Morse, D. H. 1984. How crab spiders (Araneae, Thomisidae) hunt at flowers. – J. Arachnol. 12: 307–316.

Nakata, K. 2007. Prey detection without successful capture affects spider's orb-web building behaviour. – Naturwissenschaften 94: 853–857.

Olive, C. W. 1982. Behavioral response of a sit-and-wait predator to spatial variation in foraging gain. – Ecology 63: 912–920.

Ota, K. 2018. Fight, fatigue and flight: narrowing of attention to a threat compensates for decreased anti-predator vigilance. – J. Exp. Biol. 221: jeb168047.

Patterson, M. R. 1984. Patterns of whole colony prey capture in the octocoral, *Alcyonium siderium*. – Biol. Bull. 167: 613–629.

Pruitt, J., Taylor, J. and Troupe, J. 2009. Foraging benefits and limited niche overlap promote a mixed species association between two solitary species of spider. – Behaviour 146: 1153–1170.

Rao, D. 2009. Experimental evidence for the amelioration of shadow competition in an orb-web spider through the 'ricochet' effect. – Ethology 115: 691–697.

Rayor, L. S. and Uetz, G. W. 1990. Tradeoffs in foraging success and predation risk with spatial position in colonial spiders. – Behav. Ecol. Sociobiol. 27: 77–85.

Reinert, H. K., Cundall, D. and Bushar, L. M. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. – Copeia 1984: 976–981.

Rypstra, A. L. 1989. Foraging success of solitary and aggregated spiders: insights into flock formation. – Anim. Behav. 37: 274–281.

Santucci, A. C., Cortes, C., Bettica, A. and Cortes, F. 2008. Chronic ethanol consumption in rats produces residual increases in anxiety 4 months after withdrawal. – Behav. Brain Res. 188: 24–31.

Scharf, I. 2020. Factors that can affect the spatial positioning of large and small individuals in clusters of sit-and-wait predators. – Am. Nat. 195: 649–663.

Scharf, I. 2021. The interaction between ambush predators, search patterns of herbivores, and aggregations of plants. – Behav. Ecol. 32: 1246–1255.

Scharf, I. and Ovadia, O. 2006. Factors influencing site abandonment and site selection in a sit-and-wait predator: a review of pit-building antlion larvae. – J. Insect Behav. 19: 197–218.

Scharf, I. and Ruxton, G. D. 2023a. Shadow competition: its definition, prevalence, causes and measurement. – Oikos 2023: e09774.

Scharf, I. and Ruxton, G. D. 2023b. Data from: Four scenarios in which shadow competition should be prominent and factors affecting its strength. – Dryad Digital Repository, https://doi.org/10.5061/dryad.0rxwdbs66.

Scharf, I., Golan, B. and Ovadia, O. 2009. The effect of sand depth, feeding regime, density, and body mass on the foraging behaviour of a pit-building antlion. – Ecol. Entomol. 34: 26–33.

Scharf, I., Barkae, E. D. and Ovadia, O. 2010. Response of pit-building antlions to repeated unsuccessful encounters with prey. – Anim. Behav. 79: 153–158.

Scharf, I., Gilad, T., Taichman, Y. and Subach, A. 2021. Urban pit-building insects are attracted to walls for multiple reasons. – Biology 10: 635.

Schmitz, O. J. 2000. Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system. – Oikos 89: 471–484.

Schmitz, O. J., Beckerman, A. P. and O'Brien, K. M. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. – Ecology 78: 1388–1399.

Sih, A. 2005. Predator–prey space use as an emergent outcome of a behavioral response race. – In: Barbosa, P. and Castellanos, I. (eds), Ecology of predator–prey interactions. Oxford Univ. Press. pp. 240–255.

Soibam, B., Mann, M., Liu, L., Tran, J., Lobaina, M., Kang, Y. Y., Gunaratne, G. H., Pletcher, S. and Roman, G. 2012. Open-field arena boundary is a primary object of exploration for *Drosophila*. – Brain Behav. 2: 97–108.

Uetz, G. W. 1989. The "ricochet effect" and prey capture in colonial spiders. – Oecologia 81: 154–159.

Van Damme, R. and Van Dooren, T. J. M. 1999. Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. – Anim. Behav. 57: 347–352.

Vollrath, F. 1985. Web spider's dilemma: a risky move or site dependent growth. – Oecologia 68: 69–72.

White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C. and White, C. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. – Oikos 123: 385–388.